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Management of field margins to maximize multiple ecological services

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Summary

1. Vegetative buffers in agricultural landscapes can provide a range of important ecological services, including conservation of native flora and fauna, enhancement of biological pest control and reduction of agrochemical drift. Typically, studies addressing the impact of such vegetative elements focus on one particular benefit. We investigated whether the benefits of field margins that had been established for conservation of northern bobwhite quail *Colinus virginianus* populations extended to the enhancement of biological pest control in adjacent conservation tillage cotton fields.
2. Densities of a selection of insect species and the predation and parasitism rates of insect pest species were measured in first- and second-year field margins established for bobwhite quail as well as in an adjacent cotton crop.
3. Second-year field margins yielded higher densities of all species sampled, with the exception of staphylinids and cotton aphids. Despite this, thrips and their predator, *Orius insidiosus*, were the only species that were also more abundant in the adjacent cotton field. Tachinids and *Trichogramma* and *Lygus* species, appeared to prefer the field margin vegetation over the cotton.
4. Overall, the impact of second-year margins on the cotton crop did not significantly differ from first-year margins with regard to pest occurrence or biological control.
5. Analysis of the sugar content in *Meteorus autographae*, a generalist parasitoid of Lepidoptera larvae, suggested that this species is severely food-limited in the field margins established for bobwhite quail.
6. *Synthesis and applications*. This study shows that field margins designed to specifically benefit bobwhite quail may be unsuitable for providing other ecological services. By making small adjustments in the vegetative composition of these field margins, such as adding early season nectar-producing plants, it may be feasible to combine biodiversity and pest-control benefits and thereby optimize the overall ecological services to be gained.

Key-words: ecological services, insect conservation, northern bobwhite, plant succession, vegetative buffers

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Introduction

Vegetative buffers or uncropped field margins in agricultural landscapes can provide a range of ecological services. They can provide habitat and food for wildlife (Leidner & Kidwell 2000; Cederbaum, Carroll & Cooper 2004), contribute to conservation of native flora (Keesing & Wratten 1997; Coeur *et al*. 2002) and reduce erosion, runoff and pesticide drift (Haycock, Pinay & Walker 1993; USDA 2000). It is increasingly recognized that they can also help to sustain beneficial arthropod species (Landis, Wratten & Gurr 2000; Marshall & Moonen 2002; Frank & Reichhart 2004; Gurr *et al*. 2005). In agricultural landscapes dominated by large monocultures, many arthropod species tend to suffer from a lack of nectar and pollen sources, shelter and hibernation, mating and nesting sites (Heimpel & Jervis 2005). In the absence of these vital resources, colonization of crops by predatory species is often much lower than colonization by herbivores (Altieri & Whitcomb 1979; Thies & Tscharntke 1999). This can prevent predators from controlling pest populations whose numbers are

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increasing during the critical early period of crop establishment and growth (Mayse & Price 1978; Landis, Wratten & Gurr 2000). Improving the availability of food, shelter and other resources on a more year-round basis can boost biological pest control by increasing predator populations and enhancing searching efficacy in the crop (Desender *et al*. 1981; Nicholls, Parrella & Altieri 2001; Marshall & Moonen 2002; Schmidt *et al*. 2005; Schweiger *et al*. 2005).

Indeed, it has been well-established that nectar- or pollen-feeding is essential for the reproductive success of many insect predators and parasitoids (Wäckers & van Rijn 2005). Several studies have shown vegetative buffers providing these resources improve the reproductive success of natural enemies and that this may lead to reduced populations of pest species in the crop (reviews in Gurr *et al*. 2005; Heimpel & Jervis 2005).

Although vegetative buffers may provide multiple ecological benefits, they are nevertheless typically designed with one particular function in mind. This is likely to limit their effectiveness in supporting other potential functions. For example, elements effective in wildlife conservation may be ineffective in supporting beneficial arthropods and vice versa (Kleijn *et al*. 2001). A one-dimensional approach in designing vegetative buffers not only means foregoing potential benefits but may also actually generate negative effects. Arbitrarily composed vegetative structures can increase pest populations, and populations of higher trophic level organisms, while these structures can also serve as a sink resulting in migration of beneficial species away from the crop (Landis, Wratten & Gurr 2000). Designing vegetative buffers for multiple benefits requires an understanding of the biology and ecology of all species of relevance to both the crop and the vegetative buffers.

In the USA, northern bobwhite quail (*Colinus virginianus* Galliformes: Odontophoridae) populations have declined dramatically over the last 30 years (Klimstra 1982; Brennan 1999), particularly in the south-east (Lee & Brennan 1994). Since 1996, populations have decreased 2·4% year^{-1} nationwide (Church, Sauer & Droege 1993). One apparent factor associated with these declines has been a reduction in habitat as a result of changes in land use, particularly farming (Klimstra 1982; Puckett *et al*. 1995). In response, the Georgia Department of Natural Resources (GADNR) has initiated the Bobwhite Quail Initiative (BQI), which has been widely adopted by farmers over the last few years (Leidner & Kidewell 2000). The BQI requires the establishment of a 10-m wide non-disrupted band around or through portions of a field for a period of 2–3 years. Growers are compensated for loss of yield based on the area of these buffers and on the implementation of the management required. First-year growers are required to harrow the area designated as bobwhite buffers during November–February, and non-crop plants are allowed to grow undisturbed for 2–3 years. After 3 years, the entire buffer area is disked (a turning and loosening of the soil with a series of disks to a depth of 10–15 cm) to control plant succession, as bobwhite and many other declining bird species need early succession habitats (Sauer, Hines & Fallon 2001). However, personnel involved in the BQI programme have observed quite dramatic variation in plant communities, with some dominated by exotic and invasive species, especially bermudagrass *Cynodon dactylon* L., that reduce the quality of wildlife habitat (J. Burkhart & J. Carroll, unpublished data; Burkhart 2004). The planting of specific species to offset these problems could be added to the BQI requirements, but only if it has been demonstrated to the GADNR that these species are beneficial to quail ecology and are cost-effective. The benefits of bobwhite buffers may be enhanced if they also prove effective in increasing the abundance of native predatory arthropods and in enhancing their efficacy in controlling pest insects in adjacent crops, with concomitant reductions in pesticide inputs. The age of vegetative buffers can be a factor determining the density of insect predators (Frank & Reichhart 2004), probably because of reduced disturbance of overwintering individuals.

The first objective of this study was to determine whether older or less frequently disturbed naturally regenerated field edge vegetation (i.e. first- vs. second-year bobwhite buffers), growing along the woodland edge of cotton *Gossypium hirsutum* L. (Malvales: Malvaceae) fields, increased numbers of predator and pest species in buffer vegetation. The second objective was to determine if an increase in numbers of specific species translated into increased densities in adjacent crop fields. The third objective was to investigate whether different types of vegetation found in bobwhite habitat or in a cahaba white vetch (*Vicia sativa* × *Vicia cordata* L., Fabales: Fabaceae) plot provide suitable sugar resources for adult parasitoids. To this end, specimens of a generalist parasitoid species, *Meteorus autographae* Muesebeck (Hymenoptera: Braconidae), were collected and its sugar reserves analysed.

Materials and methods

FOCAL INSECT SPECIES

All insect species sampled were potential food sources for bobwhite when they were located on the ground or on low vegetation (see Appendix S2). The noctuiids *Helicoverpa zea*, *Heliothis virescens* and *Spodoptera* spp. feed on the leaves and fruit of a number of plant species and can be serious pests in cotton. *Pseudoplusia includens* feeds on the leaves of a number of plant species, including cotton. *Pseudoplusia includens* over-winters in Florida and typically arrives in Georgia in June each year (Roberts & Douce 1999). Thrips feed on a number of plant species; they have piercing–sucking mouthparts and cause damage to the leaves and meristems of seedling cotton, primarily from the two- to five-leaf stage. *Aphis gossypii* infests a broad range of plants and is the most prevalent and economically important aphid species in cotton (O'Brien *et al*. 1993). *Lygus* species

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feed on fruits of many plant species and cause square abortion and damage to young bolls in cotton (Armstrong & Kraemer 1999). Adults and larvae of coccinellid species use aphids as their main food source but also feed on lepidopteran eggs and larvae (Schellhorn & Andow 2004). Adults and nymphs of *Orius insidiosus* are important predators of many pests in cotton, including thrips, aphids, mites, whiteflies and eggs and small larvae of lepidopterans (Knutson & Ruberson 1996). Tachinids are larval–pupal parasitoids of many lepidopteran species, including pests in cotton (Knutson & Ruberson 1996). *Trichogramma* spp. are minute egg parasitoids of primarily lepidopteran eggs (Romeis *et al*. 2005). Adults and larvae of staphylinids feed on a variety of small, soft-bodied insects and insect eggs in cotton (Knutson & Ruberson 1996).

Over 2 years, insects were sampled from five cotton fields farmed by the same grower, as well as from 10-m wide bands of first- and second-year naturally occurring vegetation that had been established at the margin of the field to provide bobwhite habitat (hereafter referred to as field margin). First-year field margins had been tilled in late November of the previous year. In 2003, four of the field margin sites were located in Mitchell Co., Georgia, USA, and two of the field margin sites were located in Colquitt Co., Georgia, approximately 8 km south-east of the other fields (see Appendix S1). All arable land surrounding the grower's land (an area of 2·56 km^2) had been planted to cotton in both years except for one peanut *Arachis hypogaea* L. field directly east of fields in Mitchell Co. In 2004, all first-year field margins in 2003 became the second-year field margins of 2004, and the second-year field margins of 2003 became the first-year field margins of 2004, as these latter sites had been disked in late autumn 2003. In 2003 Bollgard® cotton (Mitchell County Farm Service, GA) was planted in Mitchell Co. and Roundup Ready® cotton (Mitchell County Farm Service, GA) was planted in Colquit Co. In 2004 Bollgard cotton was planted in all fields. All fields had a 10-m wide grassy field road between the field margins and the cotton field. Cotton fields had a winter rye *Secale cereale* L. cover with strip tillage prior to planting, so 30% rye residue remained on the fields. The fields ranged in size from 23 to 45 ha. Field margins adjacent to woodlands were chosen as the sampling sites to minimize the potential variance associated with woodland and fence row comparisons; the fence row field margins had similar plant species as the woodland field margins but were adjacent to a dirt or paved road. A total of three first- and three second-year field margins was sampled. In 2003, three transects, each separated by 15 m, were set up at each site perpendicular to the field margin so that sampling points were 0 m (= field margin), 15 m (= 5 m from cotton field edge), 45 m and 75 m from the edge of the field margin. In 2004, a non-insecticide and a grower-determined insecticide treatments were added to the study sites, with two additional transects set up as in 2003 for each treatment. Because there were no effects of these treatments on any of the species studied, samples from 2004 were pooled for statistical analyses. We sampled insects in the field margins beginning in mid-March and continued sampling weekly until the whole plant samples were complete (see below). All plants in the field margins were identified to species and their density determined by eye. We grouped plants into two height classes (< 1 m and ≥ 1 m) for density estimates.

STICKY STRIPS

Yellow double-sided sticky strips (7·5 × 13 cm; Olson Products, Medina, OH) were placed weekly on poles along the transects, with the top of the cards at the height of the cotton plants. The poles were raised as the cotton plants grew, and the poles in the field margins were at the same height as those in the field. Insects collected on the strips were identified and counted using a dissecting microscope. We recorded species and number found on each side of the card (side facing trees and side facing field centre). There were no differences in species density with respect to the side of the card, except for Staphylindae, so we pooled the samples for statistical analyses. *Trichogramma* spp. and *Lygus* spp. were grouped, respectively, as they were difficult to identify to species from the cards. The influence of date, field margin type (first or second year), distance from the field margin (0, 15, 45 and 75 m) and their interaction on the number of insects were tested with ANOVA (SAS Institute Inc. 1998) (see Appendix S3 for results of entire model). Means were separated with Tukey's HSD, with $P = 0·05$ considered significantly different. Data were transformed as needed to meet the requirements of a normal distribution. The data from both years were combined for those species that showed no differences as a result of year.

WHOLE PLANT SAMPLES

We randomly selected cotton plants and sampled the entire plant weekly for herbivore larvae from 5 June to 1 August in 2003, and from 7 June to 31 August in 2004. At each point along the transects we sampled seven and 12 cotton plants in 2003 and 2004, respectively. All larvae found were counted, transported to the laboratory and reared on a pinto bean-based diet (King & Leppla 1984) to assess parasitism rate. Very few *Helicoverpa zea*, *Heliothis virescens* and *Spodoptera* spp. were found and we could not stabilize the variance associated with their densities. Therefore the analyses were carried out on *Pseudoplusia includens* data only. The influence of date, field margin type, distance from the field margin and their interaction on the number of *Pseudoplusia includens* larvae found was tested with ANOVA (SAS Institute Inc. 1998) (see Appendix S3 for results of entire model). On three separate dates in September of each year, we counted the number of bolls on 21 randomly chosen plants at 15, 45 and 75 m from the field margin. On each of these plants we determined boll damage from stinkbugs (mainly *Euschistus*, *Nezara* and *Acrosternum* spp.)

and Lepidoptera larvae. Parasitism levels of collected larvae and stinkbugs as well as larval boll damage were tested with chi-square analyses (SAS Institute Inc. 1998). Each year we placed irradiated *Helicoverpa zea* eggs on five plants at each distance from the field margin at each site. This was repeated three times on 15, 21 and 28 August in 2003, and on 4, 17 and 25 August in 2004, to estimate parasitism and predation rates. Single eggs were placed on a leaf near the top of the plant and left for 3 h. Subsequently, eggs were collected and incubated to determine parasitism. All eggs not recovered were considered preyed upon, most probably by *Solenopsis invicta* Buren (Hymenoptera: Formicidae) based on observations during egg collection.

SUGAR ANALYSIS

In 2004, we collected live *Meteorus autographae* from the field margins and from a cahaba white vetch (*Vicia sativa* × *Vicia cordata*) plot established at the experimental station Bellflower farm, Tift Co., Georgia. Collections were conducted weekly from 18 March to 17 April using a Vortis® suction sampler. Immediately upon collection, parasitic wasps were placed on ice, transported to the laboratory and placed individually in Eppendorf vials containing 500 µL 70% ethanol. The cahaba white vetch had been planted in November 2003 and began flowering in mid-April 2004. This species has many stipular extra-floral nectaries that start producing nectar prior to flowering (D. M. Olson, personal observation). There was some cut-leaf evening primrose *Oenothera laciniata* Hill (Myrtales: Onagraceae) present in the vetch plots during the sampling period. We collected nectar from the flowers for sugar analysis by blotting a 2-cm^2 tissue paper folded twice (1 cm^2) on several stigmas. We sampled the extra-floral nectar by clipping a 2-cm^2 tissue paper folded twice (1 cm^2) to a nectary for 3 h. Each piece of paper tissue was subsequently placed in an Eppendorf vial with 500 µL 70% ethanol solution. The predominant aphid present was the pea aphid *Acyrthosiphon pisum* Harris (Homoptera: Aphididae). We sampled pea aphid honeydew by placing each of two groups of five aphids collected from the vetch into a Petri dish with moist tissue. After 24 h, the aphids were removed and the tissue was placed in a vial with *c.* 25 mL 70% ethanol. All ethanol samples were stored at room temperature. The sugars in the samples were analysed using HPLC as described by Wäckers & Steppuhn (2003). As standards we included sorbitol, trehalose, glucose, fructose, sucrose, melezitose, raffinose, maltose and erlose. As the data for the wasp specimen were not normally distributed and the variance heterogeneity was high, non-parametric statistics were used. We tested the effect of treatment [field margin, cahaba white vetch and control (newly eclosed non-fed individuals)] on sugar levels of individuals using Kruskal–Wallis ANOVA (StatSoft Inc. 2003).

Results

FIELD MARGIN VEGETATION

In the first-year growth the predominant tall (= 1 m in height) plant species was common ragweed *Ambrosia artemisiifolia* L. (60%), while in the second-year growth it was goldenrod *Solidago canadensis* L. (32%) and dogfennel *Eupatorium capillifolium* Lam. (17%). The predominant small plant species in the first-year growth were rough Mexican clover *Richardia scabra* L. (23%), southern crabgrass *Digitaria cilaris* Retz. (17%) and Texas panicum *Panicum texanum* Buckl. (13%), whereas the second-year growth was dominated by *Digitaria cilaris* (18%), arrowleaf sida *Sida rhombifolia* L. (17%), and curlytop knotweed *Polygonum pensylvanicum* L. (17%). The predominant tree species in adjacent woodlots was loblolly pine *Pinus taeda* L. (> 90%).

STICKY STRIPS

Combining both years, there was a significant distance from the field margin by field margin type effect on thrips (d.f. = 3, $F = 7{\cdot}77$, $P < 0{\cdot}001$) and tachinids ($F = 30{\cdot}62$, $P < 0{\cdot}001$). Throughout the sampling period, more thrips were found in the field than the field margins. Also within the field, thrips numbers were higher at 45 and 75 m than 15 m from the field margin (Fig. 1a). More thrips were found in second- (mean ± SD; 176·17 ± 284·92, n = 177) than first-year (105·11 ± 95·15, n = 168) field margins in both years prior to planting the cotton. More tachinids were

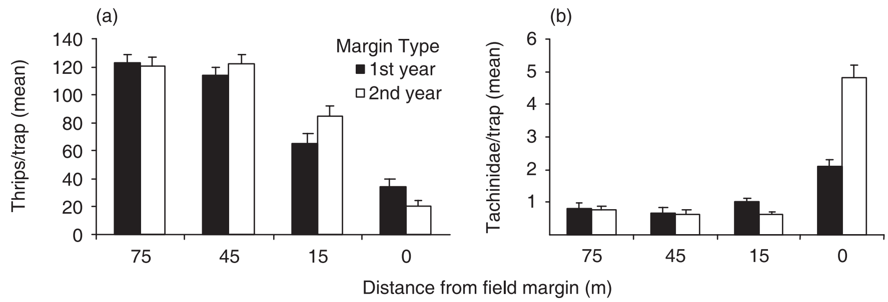

Fig. 1. The effect of distance into the cotton field from the margin (0, 15, 45 and 75 m) and field margin type (first- and second-year growth) on the mean (+ SEM) number of thrips (a) and Tachinidae (b) per sticky trap; n = 280.

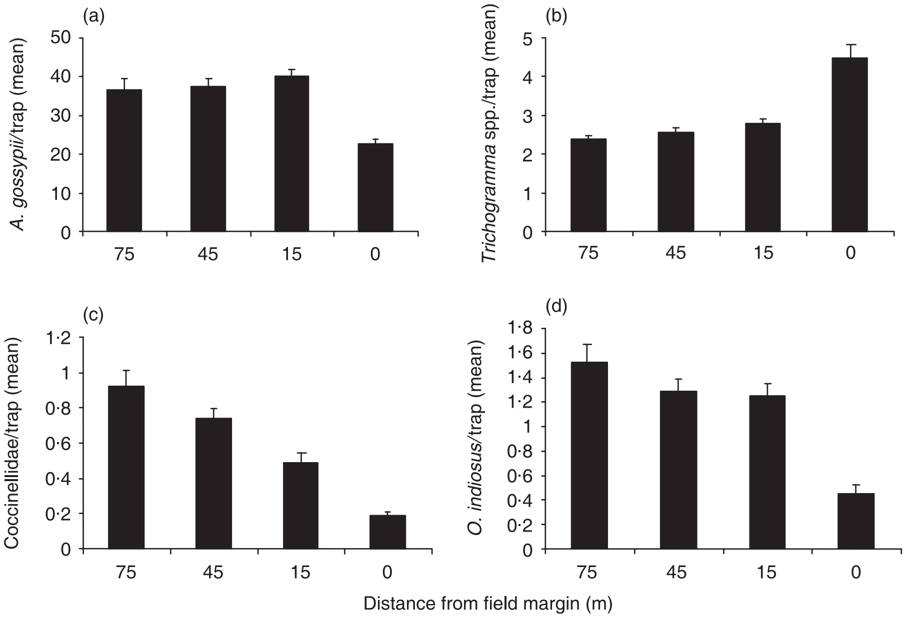

Fig. 2. The effect of distance into the cotton field from the margin (0, 15, 45 and 75 m) on the mean (+ SEM) number of aphids (a), *Trichogramma* spp. (b), Coccinellidae (c) and *Orius insidious* (d) per sticky trap; $n = 558$.

found in the field margins than within the field and in the second- than in the first-year field margins (Fig. 1b). Prior to planting the cotton, tachinid numbers were also higher in second- (2·89 ± 5·05, $n = 177$) than in first- (0·85 ± 1·09, $n = 168$) year field margins. The dominant species found were *Eucelatoria bryani* (70%), *Lespesia archippivora* (11%) and *Archytas marmoratus* (9%).

There was also an effect of distance from the field margin on *Aphis gossypii* (d.f. = 3, $F = 83·35$, $P < 0·001$), *Trichogramma* spp. ($F = 76·18$, $P < 0·001$), coccinellids ($F = 40·70$, $P < 0·001$) and *Orius insidiosus* ($F = 28·93$, $P < 0·001$) over both years. More *Aphis gossypii* were found in the field than the field margins regardless of field margin type, and their numbers were higher at 15 m compared with 45 m and 75 m from the field margin (Fig. 2a). There were no *Aphis gossypii* found in the field margins prior to planting the cotton. More *Trichogramma* spp. were found in the field margins than within the field and their numbers within the field were higher at 15 m than at 45 m and 75 m from the margin (Fig. 2b). Prior to planting the cotton, *Trichogramma* spp. were more abundant in second- (1·59 ± 1·66, $n = 177$) than in first- (0·98 ± 1·48, $n = 168$) year field margins. Coccinellids were more abundant within the field than the field margins and at 75 m than 45 m and 15 m from the field margin (Fig. 2c). The coccinellid species were *Scymnus* spp. (68%), *Harmonia axyridis* (23%) and *Hippodamia convergens* (9%), with only *Scymnus* spp. and *Harmonia axyridis* following the pattern of increased density with distance from the field margin. Only *Harmonia axyridis* was found in the field margins prior to planting the cotton, and it was more abundant in second- (0·65 ± 0·92, $n = 177$) than in first- (0·25 ± 0·60, $n = 168$) year field margins. *Orius insidiosus* was more abundant in the field than the field margin but its numbers did not differ across locations within the field (Fig. 2d). Prior to planting the cotton, *Orius insidiosus* tended to be more abundant in second- (0·33 ± 1·02, $n = 177$) than in first- (0·19 ± 0·83, $n = 168$) year field margins but this was not statistically significant ($P = 0·371$).

The effect of field margin type and distance from the field margin on the density of *Pseudoplusia includens*, staphylinids and *Lygus* spp. varied over the 2 years and their densities were higher in 2004 than in 2003 (Fig. 3). The density of *Pseudoplusia includens* was higher at 15 m than 45 m and 75 m from both the first- and second-year field margins in 2003 and was higher at 15 m and 45 m than 75 m from second-year field margins in 2004 (Fig. 3a; field margin type × distance, d.f. = 3, $F = 3·06$, $P = 0·047$ for 2003 and $F = 6·01$, $P = 0·003$ for 2004). The 2004 effect was because of a field associated with a second-year field margin that had more larvae at 45 m than 75 m from the field margin (site, d.f. = 5, $F = 8·64$, $P = 0·0001$). Removing this site also removed the effect of field margin type on larval density in 2004. Staphylinids were more abundant in second- than in first-year fields in 2003, but they were more abundant in first- than in second-year fields in 2004 (Fig. 3b; field margin type, d.f. = 1, $F = 5·26$, $P = 0·022$ for 2003 and $F = 18·29$, $P = 0·0001$ for 2004). Prior to planting the cotton in 2003, staphylinids were more abundant in second- (1·19 ± 1·32, $n = 90$) than in first-year field margins (0·50 ± 0·77, $n = 84$), and in 2004 they were more abundant in first- (2·21 ± 2·17, $n = 84$) than in second-year field margins (1·08 ± 1·37, $n = 87$). There were also more staphylinids on the side of the card facing the trees in first- and second-year fields in 2003 (card position, d.f. = 1, $F = 3·66$, $P = 0·056$) and in 2004 (d.f. = 1, $F = 11·47$, $P = 0·001$). More *Lygus* spp. were found in the field margins than in the field in both years (distance, d.f. = 3, $F = 15·06$,

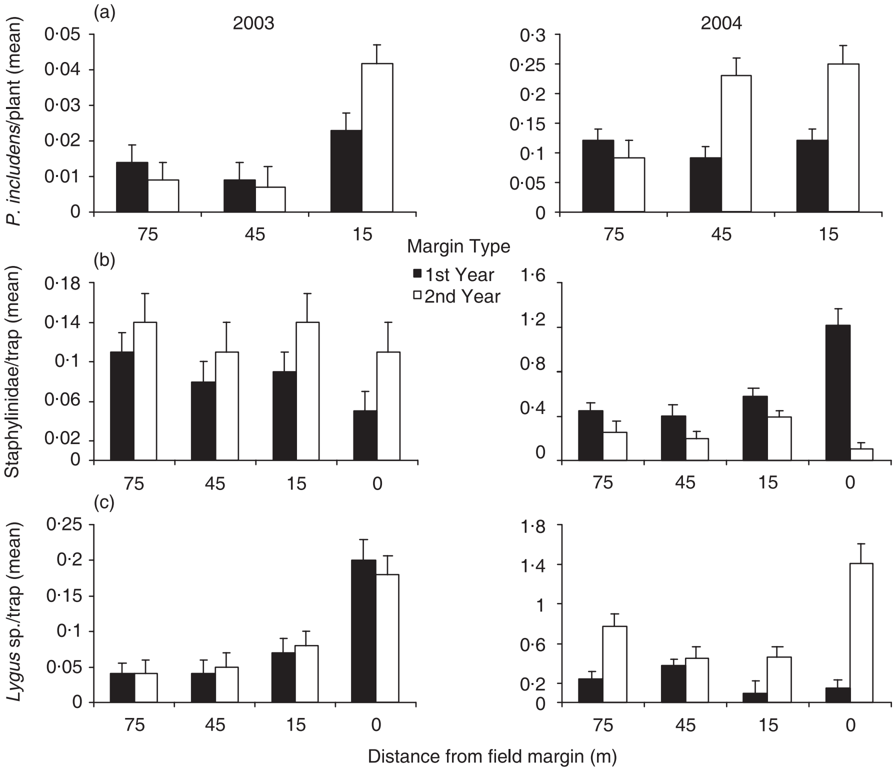

Fig. 3. The effect of distance into the cotton field from the margin (0, 15, 45 and 75 m) and field margin type (first- and second-year growth) on the mean (+ SEM) number of *Pseudoplusia includens* larvae per plant (a) Staphyinidae (b) and (c) *Lygus* spp. per sticky trap; n = 567 and 396 plants for 2003 and 2004, respectively; n = 196 and 84 sticky traps for 2003 and 2004, respectively.

$P = 0{\cdot}0001$ for 2003 and $F = 4{\cdot}12$, $P = 0{\cdot}0001$ for 2004) but they were more abundant in second- than first-year field margins in 2004 (Fig. 3c). No *Lygus* was found in the field margins prior to planting the cotton.

WHOLE PLANT SAMPLES

Seventy-four per cent of the larvae found on cotton in 2003 were *Pseudoplusia includens* (59/80), 19% were *Helicoverpa zea* and *Heliothis virescens* (15/80) and 7% were *Spodoptera* spp. (6/80). In 2004, 98% of the larvae were *Pseudoplusia includens* (563/576), 2% were *Helicoverpa zea* (11/576) and 1% were *Spodoptera* spp. (2/576). Combining both years, there were no differences in the percentage parasitism of *Pseudoplusia includens* collected on cotton (421 larvae) in first- (65/139 = 47%) and second- (138/282 = 49%) year field margins ($\chi^2 = 1{\cdot}88$, d.f. = 1, $P = 0{\cdot}170$) and at 15 m, 45 m and 75 m from the field margin ($\chi^2 = 0{\cdot}10$, d.f. = 2, $P = 0{\cdot}949$). There were no differences in boll damage from larvae in first- and second-year field margins ($\chi^2 = 0{\cdot}312$, d.f. = 1, $P = 0{\cdot}577$), and at 15 m, 45 m and 75 m from the field edge ($\chi^2 = 5{\cdot}23$, d.f. = 2, $P = 0{\cdot}073$). In 2003, there was an effect of site on boll damage from stinkbugs; the northern site in Colquitt Co. planted with Roundup Ready cotton had more stinkbug damage than the other sites (site, $\chi^2 = 14{\cdot}07$, d.f. = 5, $P = 0{\cdot}015$). Removing this site from the analysis indicated no effect of field margin type on boll damage (edge type, $\chi^2 = 1{\cdot}95$, d.f. = 1, $P = 0{\cdot}162$). Distance from the field margin in 2003 did not significantly effect boll damage from stinkbugs ($\chi^2 = 1{\cdot}65$, d.f. = 2, $P = 0{\cdot}438$). In 2004, there was no difference in boll damage from pentatomids at sites ($\chi^2 = 8{\cdot}38$, d.f. = 5, $P = 0{\cdot}136$), at first- and second-year field margin sites ($\chi^2 = 0{\cdot}407$, d.f. = 1, $P = 0{\cdot}523$), and at the three distances from the field margin ($\chi^2 = 1{\cdot}65$, d.f. = 2, $P = 0{\cdot}438$).

EGG BAITS

Combining both years, there was no effect of field margin type on the percentage of corn ear worm eggs parasitized or preyed upon ($\chi^2 = 5{\cdot}15$, d.f. = 2, $P = 0{\cdot}076$, n = 675). However, the percentage of eggs parasitized was lower at 15 m (0%) than 45 m (54%) and 75 m (46%) regardless of field margin type ($\chi^2 = 22{\cdot}36$, d.f. = 4, $P = 0{\cdot}0001$). The species reared from the eggs appeared to all be *Trichogramma pretiosum* Riley. There was no effect of the percentage of eggs preyed upon across field locations (33%, 32% and 35% for 15 m, 45 m and 75 m from the field margin, respectively).

SUGAR ANALYSIS

The average total sugar level in *Meteorus autographae* males and females from the field margins did not exceed the sugar level of unfed individuals. Parasitoids collected from cahaba white vetch plots, on the other hand, had substantially higher overall sugar levels (Table 1). Five out of the 14 field margin individuals

Table 1. Mean (± SEM) sugar levels (μg wasp^{-1}) as determined by HPLC analysis; $n = 23$, 14 and 9 wasps for vetch, field margin and control treatments, respectively. Asterisks indicate significance at $P < 0{\cdot}05$

Sugar	Vetch	Field margin	Control
Sorbitol	0·76 ± 0·08*	0·24 ± 0·05*	0·68 ± 0·09
Trehalose	0·16 ± 0·07	0·06 ± 0·00	0·00 ± 0·00
Glucose	6·70 ± 2·14*	4·11 ± 1·41*	7·38 ± 0·73
Fructose	6·92 ± 2·03*	3·38 ± 1·37	0·08 ± 0·00*
Sucrose	2·86 ± 0·65*	0·24 ± 0·08*	0·04 ± 0·00*
Erlose†	0·31 ± 0·13	0·09 ± 0·05	0·00 ± 0·00
Melzitose	0·66 ± 0·43*	0·03 ± 0·00	0·00 ± 0·00
Raffinose†	0·10 ± 0·00*	0·03 ± 0·00	0·00 ± 0·00
Maltose	1·20 ± 0·22	0·34 ± 0·16*	1·08 ± 0·17
Total	29·66 ± 5·11*	8·53 ± 3·07*	9·26 ± 0·95*

†Signature sugars for honeydew.

Table 2. Mean (± SD) percentage sugar levels as determined by HPLC analysis; $n = 7$, 4 and 2 samples with six aphids per sample for vetch extra floral nectar, cut-leaf evening primrose floral nectar and pea aphid honeydew, respectively

Sugar	Extra-floral	Cut-leaf	Pea aphid
Sorbitol	2·20 ± 1·49	20·13 ± 8·60	21·08 ± 5·31
Trehalose	0·00 ± 0·00	0·00 ± 0·00	1·66 ± 0·48
Glucose	29·18 ± 4·25	32·22 ± 9·76	53·54 ± 0·42
Fructose	27·27 ± 5·84	32·13 ± 11·64	0·50 ± 0·10
Sucrose	40·52 ± 9·83	15·52 ± 15·78	1·55 ± 0·38
Maltose	0·44 ± 0·49	0·00 ± 0·00	21·68 ± 3·93
Total	100·00	100·00	100·00

analysed contained less than 1·5 μg sugars, which indicated near energetic exhaustion. In comparison, total sugar levels in unfed control individuals ranged from 5·4 to 12·5 μg, while 22 out of 23 individuals collected from the vetch plots contained more than 6·4 μg sugars (with the recorded maximum being 84·6 μg). Only four out of the 14 field margin individuals analysed showed elevated overall sugar levels relative to the control, indicating sugar feeding. Four others could be identified as having fed based on their elevated fructose levels (Olson *et al*. 2000; Wäckers & Steppuhn 2003). Three out of these 14 parasitoids showed some level of erlose and/or raffinose, indicating that these wasps had fed on aphid honeydew (Table 1). Within the cahaba white vetch plot, both the floral and extra-floral nectar have a balanced glucose/fructose ratio, whereas the pea aphid honeydew was extremely glucose biased, with maltose also being a glucose–glucose disaccharide (Table 2). Twelve out of the 23 parasitoids collected from the vetch showed extremely glucose-biased sugar profiles, usually in combination with some level of aphid-synthesized sugars, indicating that they had fed solely on pea aphid honeydew. Interestingly, the four individuals with the highest sugar levels (> 70 μg) showed a balanced glucose–fructose ratio and relatively high sucrose levels, indicating that they had primarily consumed nectar (Table 2).

Discussion

Vegetative field margin buffers in agricultural landscapes have positive effects on bobwhite populations (USDA 2004) but our study suggests that these bobwhite field margins provide limited benefits in terms of enhancing the biological control of crop pests in adjacent crops. All insect species, except staphylinids and *Aphis gossypii*, were, as expected, more abundant in less frequently disturbed field margins. Nevertheless, this increase in the margins only appeared to be reflected within the field through associated increases in thrips and possibly *Orius insidiosus*.

The distribution of Tachinid and *Trichogramma* spp. parasitoids suggests that these species have a preference for field margins and that these areas serve as a sink rather than a source for these parasitoids. In addition, *Trichogramma* spp. densities near the field margins exceeded densities in the centre of the field, suggesting some 'spill-over' into the field may occur. However, this did not translate into increased parasitism. Parasitism of *Helicoverpa zea* eggs near the field margins was actually lower than in the field centre. It is possible that this reflects sex-specific habitat requirements, with males being retained by the field margin and host-searching females dispersing further into the field.

Frank & Reichhart (2004) found that diversity and abundance of four out of five staphylynid species were consistently higher in second- and third-year wildflower strips compared with first-year strips. The lack of consistent captures of staphylinids in our study suggests the population distribution was primarily influenced by factors other than the succession stage of field margins. However, increased densities of these species within field margins prior to planting cotton and greater abundance on the tree side of the sticky strips suggests colonization from field margins.

Less abundant species in field margins (*Hippodamia convergens*, *Scymnus* spp. and *Aphis gossypii*) probably colonize the cotton fields from other areas and may not respond to field margins regardless of succession stage. A number of taxa were more abundant in less frequently disturbed field margins, *Orius insidiosus*, thrips, *Trichogramma* spp., *Harmonia axyridis* and tachinids, and the latter three were not found in greater numbers in cotton fields adjacent to less disturbed field margins. This could indicate that more than 2 undisturbed years are needed for populations to build up to levels that can impact adjacent fields. Alternatively, the vegetation in the field margins may not have provided sufficient resources, such as alternative hosts, food, mates and shelter, for these insect species. Wäckers & Steppuhn (2003) were able to demonstrate that parasitoids collected adjacent to a flowering field border had higher levels of sugar, the adult energy source, than individuals collected in control fields. In the present study, sugar levels in *Meteorus autographae* collected from field margins did not exceed sugar levels in unfed specimens. Parasitoids collected from cahaba white vetch plots, on the other hand, showed an average sugar level more than three times the average levels in the two other treatments. This strongly suggests that the variety of plant species in the bobwhite field margins contribute little or nothing to the nutrition of this parasitoid, whereas a single suitable plant such as vetch can have quite an impact. This contradicts the commonly held notion that conservation biological control through habitat management benefits from high diversity *per se* (for a critical review Gurr *et al*. 2004). Arthropod diversity is often highly correlated with plant species diversity; however, responses to plant diversity may differ among arthropod groups (Knop *et al*. 2006). Our results underline that these individual responses may be understood in terms of arthropod-specific resource requirements.

Meteorus autographae collected in bobwhite quail field margins were clearly sugar-limited, indicating lack of suitable sugar sources in these field margins. Adding specific nectar-secreting plant species to naturally regenerated field margins could be an effective method for improving biological pest control in adjacent crops, both by increasing the ratio of beneficials to pest insects and by enhancing searching efficacy of predators and parasitoids. In addition to nectar and pollen availability, insect communities are obviously also shaped by the presence or absence of other resources (Wilkinson & Landis 2005). Also, a growing number of studies indicate that landscape complexity, land-use intensity and vegetative connectivity can shape insect population structure at the local or field scale (Roschewitz *et al*. 2005; Schmidt *et al*. 2005; Schweiger *et al*. 2005). Therefore, optimum habitat manipulations at the field level may also depend on factors at the landscape scale.

Cahaba white vetch readily reseeds and harbours many beneficial species early in the year (D. M. Olson, unpublished data), and proved to be a good food source for *Meteorus autographae*, mainly through the floral and extra-floral nectaries but also through the presence of pea aphid honeydew. The vetch species also harbours many *Lygus* spp., so careful consideration must be made prior to the use of this plant species. However, we found very little evidence of cotton fruit damage or fruit abortion on cotton plants adjacent to the vetch plots (D. M. Olson, unpublished data). Cederbaum, Carroll & Cooper (2004) found significantly higher densities of birds (often 10–12 times as many) and arthropods in clover compared with areas with no clover, and bobwhite consumed larger amounts of both insects and seeds in strip-clover fields compared with conventional fields (J. Carroll, unpublished data). As cahaba white vetch is a leguminous species, as well as harbouring high arthropod densities and producing large seeds, it is probably of benefit to bobwhite and other birds.

Vegetative field margins have potential as dual-service sites, serving bobwhite and other birds while also providing biological control agents for crop pest control. Our study indicates that the addition of specific nectar-secreting plant species to naturally regenerated field margins can maximize benefits of field margin sites to both bobwhite and beneficial insects. However, further studies are needed to evaluate the effects of such additions on both bird and insect communities.

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Supplementary material

The following supplementary material is available as part of the online article (full text) from http://w.w.w.blackwell-synergy.com.

Appendix S1. Aerial photographs of the study sites.

Appendix S2. List of insect species sampled.

Appendix S3. ANOVA results of entire statistical model for insect species sampled.